
JOURNAL OF THE ARNOLD ARBORETUM

VOL. 59

APRIL 1978

NUMBER 2

FORM OF THE PERFORATION PLATES IN THE WIDE VESSELS OF METAXYLEM IN PALMS

LARRY H. KLOTZ

THIS ARTICLE SUMMARIZES the results of a survey (Klotz, 1977) of the form of the perforation plates in the wide vessels of the metaxylem in the family *Arecaceae*, the palms. The objective is to compare and contrast this feature in petiole, stem, and root among the taxonomic and ecological groups of palms.

The form of tracheary elements is an important character in plant systematics (Carlquist, 1975), and its significance in plant physiology and autecology is recognized in regard to the efficiency and safety of water conduction (Zimmermann, 1978). The present work is complementary to the series of intensive studies that Cheadle has produced on tracheary elements within various other families of monocotyledons (e.g., Cheadle & Kosakai, 1975). Before the present study was undertaken, the palms were among the large families of monocotyledons that remained to be examined in detail, although Cheadle (1942), Mahabalé (1959), and Tomlinson (1961, 1965, 1966, 1969) had published data on perforation plates in various species of palms.

A large family of about 2800 species in over 200 genera (Moore, 1973), the palms deserve thorough anatomical investigation for several reasons. They are important economically for various natural products and for ornament. Unfortunately, some of the cultivated species are currently being ravaged by lethal diseases (Fisher, 1975). Palms compose a significant part of the vegetation in many kinds of tropical and subtropical ecosystems (Moore, 1973). Finally, the palms are of theoretical importance in plant systematics for their combination of primitive and advanced features (Moore & Uhl, 1973), and in plant anatomy and physiology for their large "woody" habit and their complicated vascular structure (Tomlinson & Zimmermann, 1967).

MATERIALS AND METHODS

Tracheary elements were examined in the petiole or the rachis of 209 species, the stem of 169 species, and the root of 136 species of palms. All

15 of the major taxonomic groups in the family (Moore, 1973) were represented. Specimens of some genera were difficult or impossible to obtain, especially stems of large, single-stemmed palms. All three vegetative organs were sampled in at least one species of every genus for which material was available except those species within the large arecoid major group. In this group, all but one of the generic alliances were sampled; and in the alliances with more than one genus, species from two or more genera were examined, depending on the size of the alliance. Within two of the larger genera, *Bactris* and *Chamaedorea*, species were selected from each of the principal subgenera or sections.

Specimens were obtained from natural populations in native habitats or from cultivated collections in botanical gardens, and where possible were vouchered with an herbarium specimen. Collection data for the specimens and the authors of the species are available (Klotz, 1977).¹

The specimens were taken from plants with mature leaf morphology and stem diameter. The segments of first-order roots preferred were fairly straight and had few or no branches. Most of the stems were sampled within the central one-third of the stem diameter. The position of the sample along the length of the stem was usually not known, but the middle of the length was selected where possible. Petioles were sampled in the central (i.e., interior) part, preferably at midlength. In species lacking pronounced petioles, a segment of the proximal part of the rachis, between insertions of the pinnae, was examined.

Specimens fixed in FAA (Johansen, 1940) and dried herbarium specimens were used. The latter were softened by boiling them in water. Each specimen was sectioned transversely with razor blades or a sliding microtome. The remaining portion was cut into slivers that were macerated in Jeffrey's solution (Johansen, 1940) and stained with Delafield's hematoxylin. Additional details of the procedure are given by Klotz (1977).

One piece from one organ of an individual usually constituted the sample. In a few species, similar samples from two different collections were examined. Using the same piece for both transverse sections and maceration allowed correlation of cells in the maceration with the position of comparable cells in the corresponding transverse section. For almost all specimens at least 10 intact wide vessel elements of metaxylem were studied. The characteristics of the perforation plates are thus based on 20 or more perforation plates from 10 or more wide vessel elements. Successive elements of one vessel as well as vessel elements from several different vascular bundles were examined. Narrow tracheary elements were also obtained.

¹ Specimens from stems of three species of borassoid palms were examined after completion of the thesis (Klotz, 1977) but are included in the tabulations of this article: *Bismarckia nobilis* — Subtropical Horticultural Research Station, U. S. Dept. Agriculture, Miami, Fla., P. I. 106-556-7514; *Borassus aethiopum*; and *Hyphaene guineensis*. All three specimens were collected by P. B. Tomlinson. The latter two had been examined by him previously and listed with author citations and collection data (Tomlinson, 1961).

DEFINITIONS AND CATEGORIES

TRACHEIDS AND VESSEL ELEMENTS. In this study vessel elements are distinguished from tracheids on the basis of the shape of the cell and the configuration of the secondary wall. More specifically, vessel elements have end walls in which the apertures between the bars of secondary wall are wider than the comparable apertures on the lateral walls — i.e., the intervessel pits. Such end walls are either true perforation plates or, at least, distinctive contact areas between successive tracheary elements.

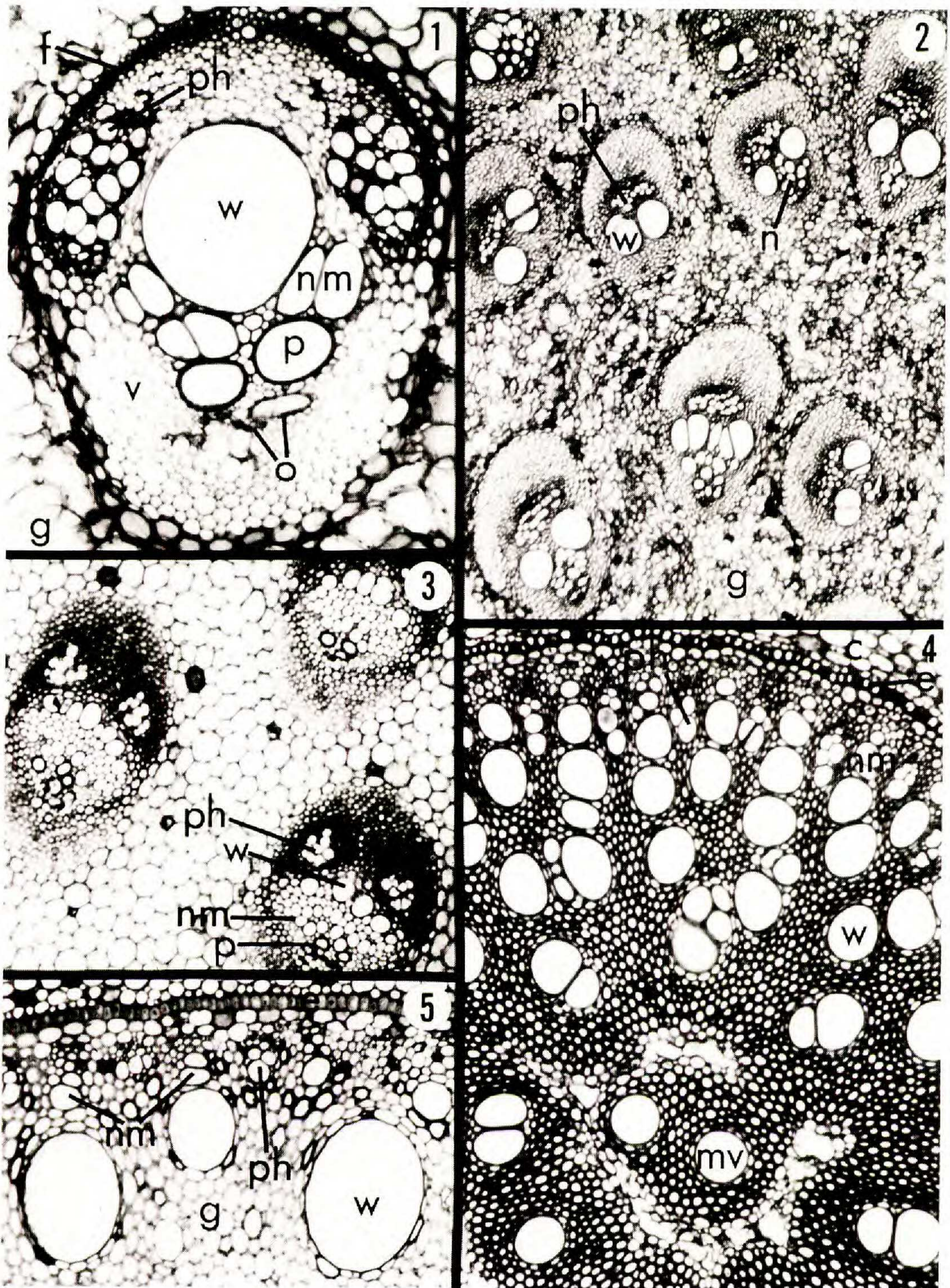
By definition, tracheids are imperforate cells with only pit-pairs on their contiguous walls, whereas vessel elements are perforate in certain areas of contiguity with other vessel elements (Esau, 1965). However, this distinction is often difficult to make because the difference between tracheid and vessel element or between pit and perforation can be a matter of degree. Distinct pit membranes across the apertures of the end walls of the wide tracheary elements were usually not observed in longitudinal sections with light microscopy, but it is possible that embedding in celloidin or some other plastic might have yielded positive results in more specimens. Scanning electronmicroscopy (SEM) reveals that variable amounts of hydrolyzed primary wall (i.e., pit membrane) can remain across perforation apertures in palms (Klotz, 1977; Parthasarathy & Klotz, 1976).

PRIMITIVE AND ADVANCED. The terms “primitive” and “advanced” are used to express the degree of resemblance of vessel elements to tracheids. Thus, primitive vessel elements have long, extremely oblique or very oblique end walls in which the perforation plates have many bars that are closely spaced, and advanced vessel elements have slightly oblique to transverse end walls on which the bars are few or absent (Cheadle, 1943a).

NARROW AND WIDE TRACHEARY ELEMENTS. In vascular bundles of the shoot, one (FIGURE 1), two (FIGURE 2), or more than two (FIGURE 3) of the tracheary elements of the metaxylem are markedly wider than the other tracheary elements. In roots, the tracheary elements toward the center of the root are usually wider than those nearer the endodermis (FIGURES 4, 5). The widest tracheary elements in the vascular bundles of the shoot or in the stele of the root are termed “wide”; the remainder are termed “narrow.”

END WALL SLOPE. Cheadle’s (1943a) classification of end wall slopes is employed with the addition of the category “extremely oblique” for especially long end walls:

e (extremely oblique)	end wall > 10 times as long as cell width
v (very oblique)	end wall > 5 to ≤ 10 times as long as cell width
o (oblique)	end wall > 2 to ≤ 5 times as long as cell width
s (slightly oblique)	end wall > 1 to ≤ 2 times as long as cell width
t (transverse)	end wall perpendicular to lateral wall



FIGURES 1-5. Transverse sections. 1, vascular bundle from petiole of *Mauritia vinifera*, $\times 82$. Some tracheary elements of protoxylem obliterated (o). 2, central part of stem of *Ceroxylon crispum*, $\times 20$. Most axial bundles with two wide vessels in metaxylem. 3, petiole of *Rhipidophyllum hystrix*, $\times 82$. Several wide vessels in metaxylem. 4, root of *Trithrinax brasiliensis*, $\times 75$. Several rows of wide vessels. Medullary vessels present (mv). 5, root of *Mauritiella pacifica*, $\times 82$. One row of wide vessels. (c, cortex; e, endodermis; f, fibers; g, ground tissue; mv, medullary vessel; n, narrow tracheary elements; nm, narrow tracheary elements of metaxylem; o, obliterated tracheary elements of protoxylem; p, tracheary elements of protoxylem; ph, phloem; v, parenchyma of vascular bundle; w, wide vessel of metaxylem.)

The distinction between transverse and slightly oblique is somewhat subjective but is adhered to rather strictly. In many samples, especially those from roots, end walls range from apparently perpendicular to the length of the cell to only a few (≤ 15) degrees from the perpendicular — i.e., they are very slightly oblique.

The overall or net slope of curved end walls was estimated. Ligules (FIGURES 36–38) were not included in determining slope.

Two methods were devised to summarize the data. First, proportional frequencies were determined for the five categories of slope for each organ in each major group. Each species was given equal weight, even if more vessel elements had been obtained from some specimens than from others. The proportional frequencies are presented as histograms (FIGURE 41). Second, “slope indexes” (TABLE 1) were calculated for each organ according to the formula:

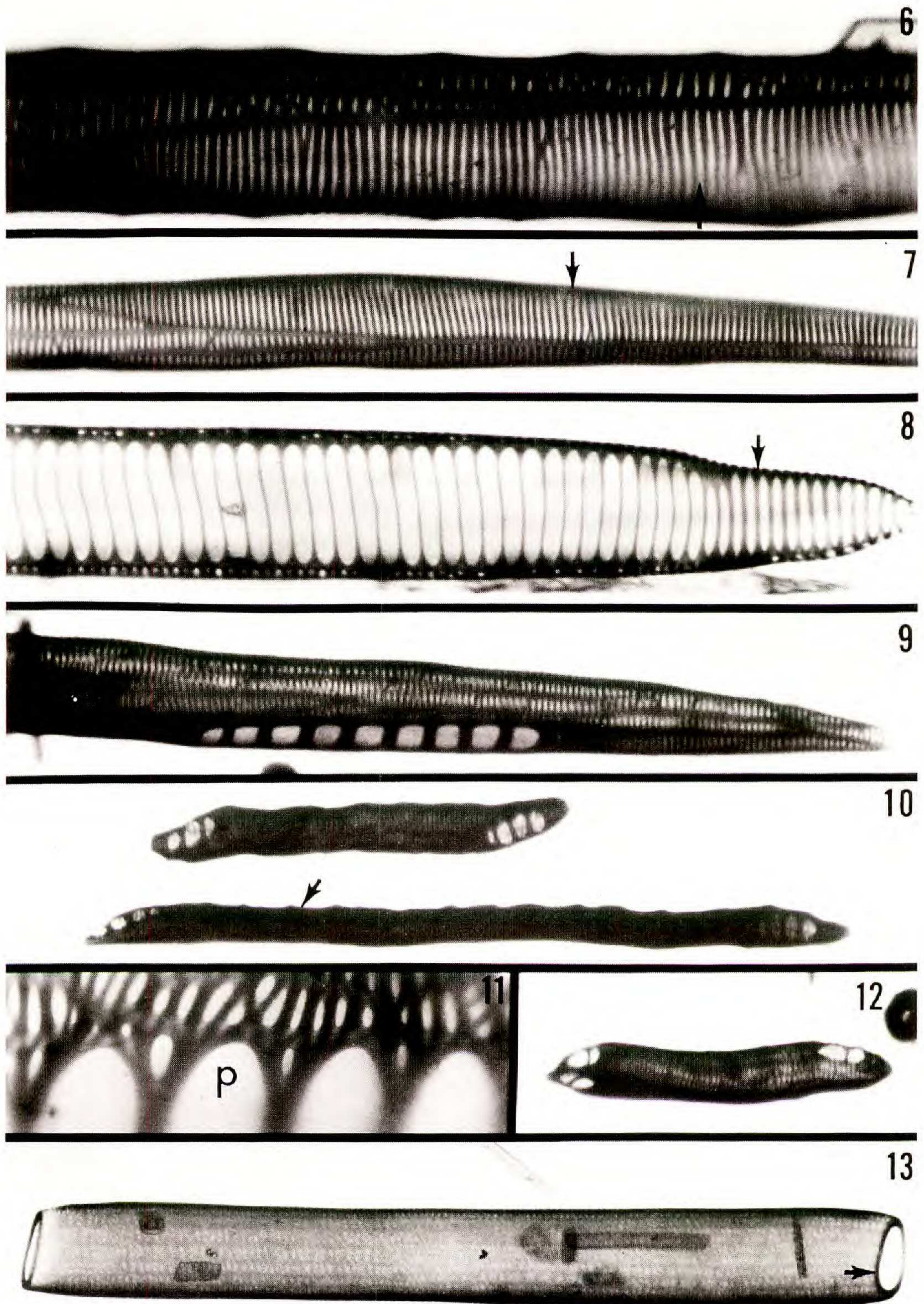
$$\begin{aligned} \text{slope index} \times 100 = & 0 (\% \text{ tracheids}) + 1 (\% \text{ extremely} \\ & \text{oblique end walls}) + 2 (\% \text{ very oblique end walls}) + 3 (\% \\ & \text{oblique end walls}) + 4 (\% \text{ slightly oblique end walls}) + 5 \\ & (\% \text{ transverse end walls}) \end{aligned}$$

Average slope indexes were calculated for the organs in each of the major groups, and “total slope indexes” were calculated by adding the average slope indexes for the three organs. In this way, a single numerical value was obtained to summarize the average slope of the end walls in each of the major groups. In TABLE 1, the total slope indexes of the major groups are listed in order of increasing value (or decreasing obliqueness).

In the iriarteoid major group, the average slope index for the aerial roots is lower than that for the subterranean roots. Since the two kinds of roots are not from the same species, total slope indexes for the iriarteoid palms are calculated both ways (TABLE 1).

“SPECIALIZATION VALUES.” “Specialization values” are assigned to the samples of perforation plates of the wide vessel elements of metaxylem according to the following system, which includes categories for describing the relative spacing of bars of secondary wall in multiple perforation plates. This system differs from the one invented by Cheadle for other groups of monocotyledons (e.g., Cheadle & Kosakai, 1975) in order to express the data for palms in more detail.

- 0 — tracheids only — definite vessels not observed
- 1 — multiple perforation plates with “pitlike” perforations that span ≤ 1 vessel–parenchyma pit on the adjacent lateral wall (FIGURES 6, 7)
- 2 — multiple perforation plates with “narrow” perforations that span > 1 to ≤ 2 vessel–parenchyma pits (FIGURE 8)
- 3 — multiple perforation plates with “medium-size” perforations that span > 2 to ≤ 5 vessel–parenchyma pits (FIGURES 9, 11, 23)
- 4 — multiple perforation plates with “wide” perforations that span > 5 vessel–parenchyma pits (FIGURE 15), or with ≤ 3 bars



FIGURES 6-13. Isolated wide tracheary elements of metaxylem. 6, petiole of *Pinanga* sp. (*H. E. Moore 9112*), $\times 240$. Arrow indicates end wall with apertures more closely spaced than pits of adjacent lateral wall. 7, stem of *Wendlandiella polyclada*, $\times 240$. Arrow indicates end wall with apertures about as closely spaced as pits of adjacent lateral wall. 8, root of *Physokentia rosea*, $\times 240$. End wall with each perforation spanning about two pits of adjacent lateral wall. Arrow indicates narrower apertures, possibly intervessel pits, in distal part of end wall. 9, stem of *Lepidocaryum gracile*, $\times 140$. End wall in which perforations, separated by wide bars, each span about five pits of adjacent

TABLE 1. Total average slope indexes for the major groups.

MAJOR GROUP		SLOPE INDEX
XI.	Podococcoid	7.3
IX.	Chamaedoreoid: smaller species	7.4
IX.	Chamaedoreoid: total	8.1
XV.	Phytelephantoid *	8.2
V.	Nypoid	8.6
XIV.	Geonomoid	8.9
VIII.	Ceroxyloid	9.1
X.	Iriarteoid: including aerial roots	9.1
XII.	Arecoid	9.3
X.	Iriarteoid: including subterranean roots	9.4
IX.	Chamaedoreoid: larger species	10.0
II.	Phoenicoid	10.1
IV.	Lepidocaryoid: non-lianas	10.9
VII.	Pseudophoenicoid	11.2
I.	Coryphoid	11.2
XIII.	Cocosoid	11.2
III.	Borassoid	11.4
VI.	Caryotoid	11.5
V.	Lepidocaryoid: total	12.0
IV.	Lepidocaryoid: lianas	12.6

* Including *Ammandra*, with only tracheids in the stem.

5 — mixture of multiple perforation plates (as in #4) and simple perforation plates

6 — simple perforation plates only (FIGURE 13)

Samples that span two adjacent categories are assigned values of "½"; for example, "3½" expresses samples of multiple perforation plates with bars of "medium" to "wide" spacing, and "5½" expresses samples in which the end walls bear one or no bars. Mixed samples that span a wider range of categories are designated with "a":

2½a — perforation plates in sample range from 1 to 4

3a — from 2 to 4

3½a — from 2 to 5 (or 6)

4a — from 3 to 5 (or 6)

lateral wall. 10, stem of *Chamaerops humilis*, × 100. Vessel elements with slightly crooked or scalloped (arrow) lateral walls. Perforation plates have few bars. 11, stem of *Euterpe cuatrecasana*, × 750. Detail of vessel element with each perforation (p) spanning about five pits of adjacent lateral wall. 12, stem of *Rhapidophyllum hystrix*, × 120. Vessel element with one bar in each of three perforation plates. 13, stem of *Calamus muelleri*, × 100. Vessel element with simple perforation plates. Arrow indicates broad flange of secondary wall around perforation.

A similar procedure was applied to Cheadle's system of specialization values (Cheadle, 1955), which considers only the relative abundance of multiple perforation plates versus that of simple perforation plates:

0 — tracheids only	} mixed multiple and simple perforation plates
1 — multiple perforation plates only	
2 — $\leq 1/3$ simple perforation plates	
3 — $> 1/3$ simple to $\leq 2/3$ simple	
4 — $> 2/3$ simple	
5 — simple perforation plates only	

The values refer only to the wide tracheary elements of the metaxylem. For values 2 through 4, Cheadle does not specify exact percentages but lets 2 stand for "mostly scalariform"; 3, for "about equal scalariform and simple"; and 4, for "mostly simple" (Cheadle & Kosakai, 1975).

Within the taxonomic groups of palms, the means of the specialization values were calculated for each organ and were plotted as points (FIGURES 42, 43). A vertical line through a point indicates the range of specialization

TABLE 2. Total average specialization values for the major groups.

AUTHOR'S SYSTEM		CHEADLE'S SYSTEM	
Chamaedoreoid: small species	5.1	Nypoid	3.0
		Chamaedoreoid: small species	3.0
Iriarteoid: aerial roots	6.2		
Chamaedoreoid: total	6.3	Chamaedoreoid: total	3.7
Podococcoid	6.5	Iriarteoid: aerial roots	3.8
Iriarteoid: subterranean roots	7.1		
		Iriarteoid: subterranean roots	5.0
Nypoid	8.0	Chamaedoreoid: large species	5.5
Ceroxyloid	8.3	Arecoid	5.8
Geonomoid	8.6	Pseudophoenicoid	6.0
Arecoid	9.0	Podococcoid	6.0
Phytelephantoid *	9.0	Geonomoid	6.0
		Ceroxyloid	6.5
Chamaedoreoid: large species	9.7	Phytelephantoid *	6.7
Pseudophoenicoid	10.5	Caryotoid	7.6
		Cocosoid	7.8
Coryphoid	11.9	Phoenicoid	8.0
Caryotoid	11.9	Lepidocaryoid: non-lianas	8.6
Phoenicoid	12.0	Coryphoid	8.8
Cocosoid	12.1		
		Borassoid	10.0
Lepidocaryoid: non-lianas	13.2		
Borassoid	13.4	Lepidocaryoid: total	10.8
Lepidocaryoid: total	14.5	Lepidocaryoid: lianas	11.9
Lepidocaryoid: lianas	15.0		

* Including *Ammandra*, with only tracheids in the stem.

values for the organ in the group. The three points on each chart (for petiole, stem, and root) are connected by lines merely to make the patterns easier to perceive.

The specialization values were further summarized by adding the averaged values for petiole, stem, and root in the major groups of palms (TABLE 2). In the iriarteoid major group, the average value for the aerial roots is lower than that for the subterranean roots. Since the two kinds of roots are not from the same species, the total average specialization values for the iriarteoid palms are calculated both ways.

OBSERVATIONS

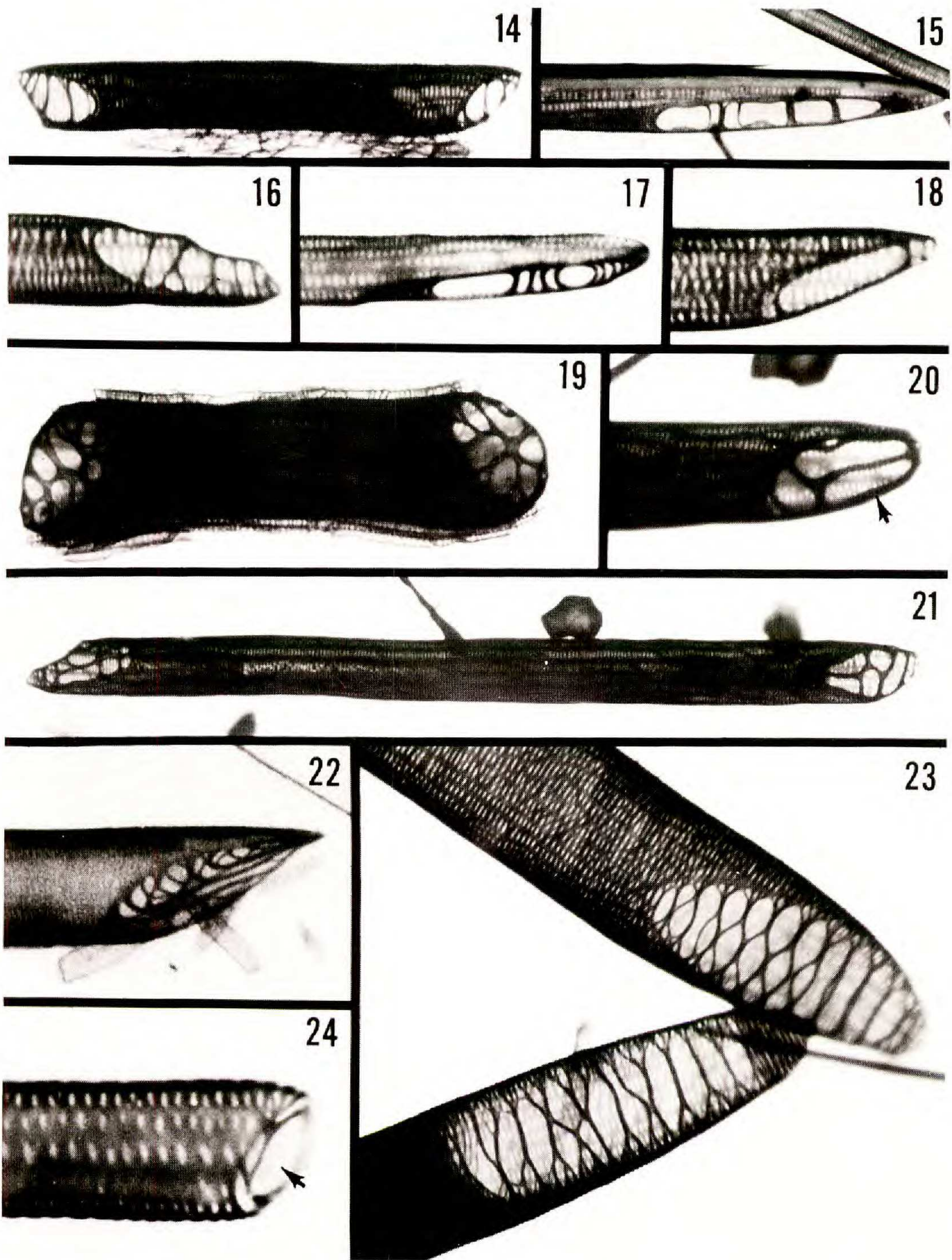
KINDS OF PERFORATION PLATES. The wide tracheary elements of the metaxylem are vessel elements, except possibly in the rhizomatous stem of the phytelephantoid palm *Ammandra decasperma*. Multiple and/or simple perforation plates occur in the wide vessels.² Most of the multiple perforation plates are basically scalariform. The most tracheid-like variety contains many bars on steeply sloping end walls in which the perforations are less widely spaced than the adjacent vessel-parenchyma pits of the lateral walls, but more widely spaced than the intervessel pits (FIGURE 6). This primitive variety grades into perforations that are about as closely spaced as the adjacent vessel-parenchyma pits of the lateral walls (FIGURE 7). In successive forms there is a gradation toward fewer, more widely spaced bars (FIGURES 8-11, 14-18); to only one bar (FIGURE 12); and finally, in the advanced extreme of the series, to no bars (FIGURE 13). Paralleling this gradation is a general decrease in the slope of the end wall.

Where perforations are narrow, the bars of the perforation plates are usually spaced evenly; but with wider spacing of bars, the bars tend increasingly toward irregular spacing (FIGURES 14-18). Bars of perforation plates frequently branch and anastomose to varying degrees (FIGURES 23, 28, 29) and rarely end blindly (FIGURES 28, 31).

The gyres of secondary wall that compose the bars of a perforation plate sometimes appear incompletely "fused" to varying degrees (FIGURE 30). The apertures between such "unfused" gyres are often no wider than the pits of the lateral walls, but sometimes they approach the width of the major perforations.

Reticulate perforation plates are the other basic type of multiple perforation plate (FIGURES 19-22, 24). An extreme variation of this type consists of only one bar, which is oriented longitudinally rather than transversely in the perforation plate. In another distinctive variation, a large, central perforation is surrounded by smaller apertures that are larger than the pits of the lateral walls (FIGURE 24). Reticulate perforation plates intergrade with scalariform perforation plates through a great diversity of forms. These intermediate, "scalariform-reticulate" configurations range

² The terminology for perforation plates is from Esau (1965).



FIGURES 14-24. Vessel elements of metaxylem. Figure 15 is narrow vessel element; the others are wide vessel elements. 14-18, scalariform perforation plates: 14, stem of *Pseudophoenix sargentii*, $\times 82$, few bars, unevenly spaced; 15, root of *Calamus perakensis*, $\times 260$, few bars, unevenly spaced and unequal in width; 16, root of *Aiphanes* sp., $\times 140$, few bars, unevenly spaced; 17, root of *Chelyocarpus dianeurus*, $\times 140$, bars very unevenly spaced; 18, root of *Physokentia rosea*, $\times 140$, one large, central perforation. 19-22, reticulate perforation plates: 19, stem of *Sclerosperma mannii*, $\times 88$; 20, stem of *Lepidocaryum gracile*, $\times 100$ (arrow indicates flange of secondary wall surrounding most of perforation plate); 21, stem of *Lepidocaryum gracile*, $\times 66$; 22, petiole of *Daemonorops grandis*, $\times 300$. 23, scalariform-reticulate perforation plates: stem of *Clinostigma savaiiense*, $\times 75$, branching and anastomosing of bars rather regular (upper ves-

from highly regular, lattice-like arrangements of many bars spaced rather closely (FIGURES 25, 26) to arrangements in which the spacing of the bars is more sparse and/or irregular (FIGURES 23, 27, 29, 31).

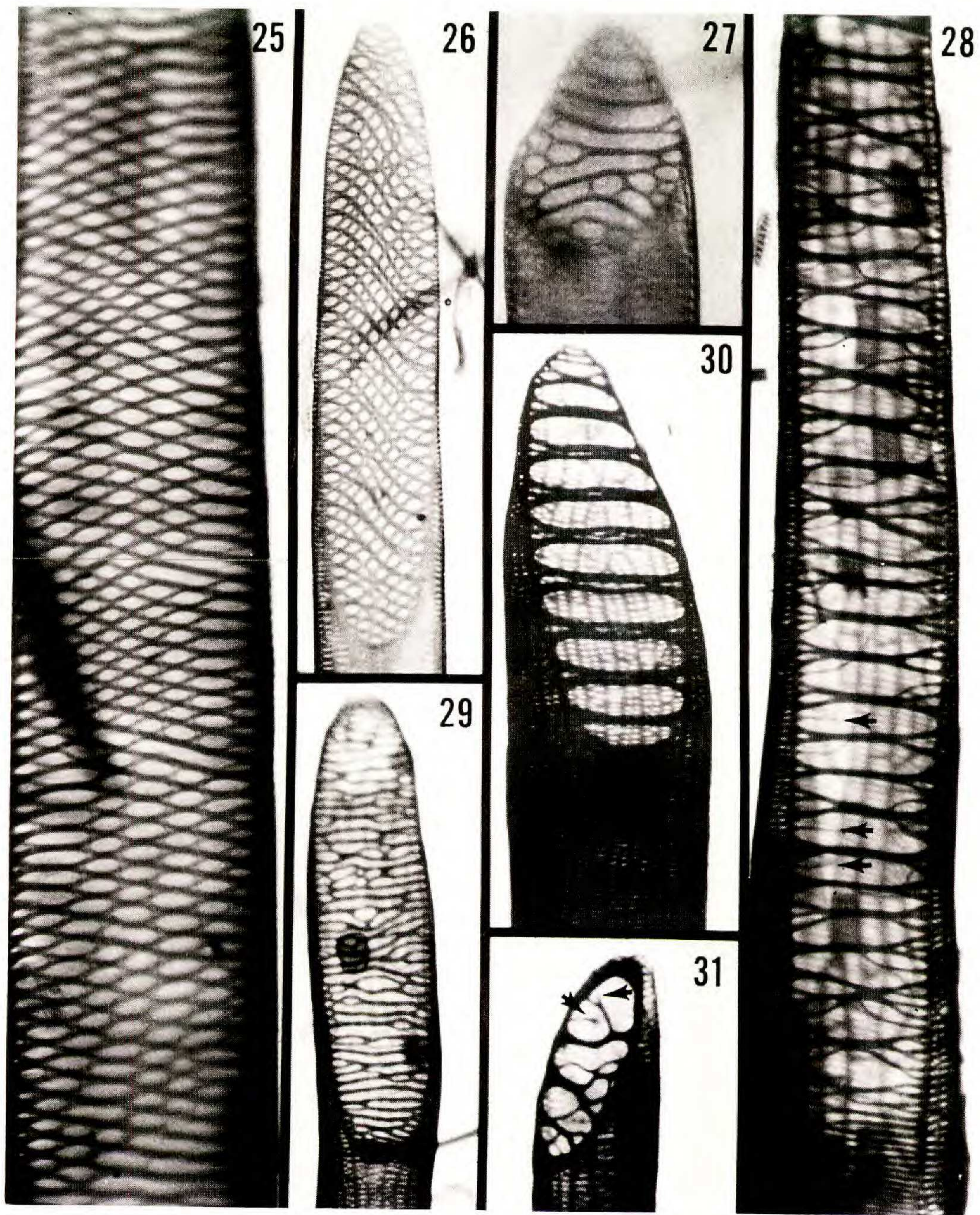
Perforation plates also vary in other ways. Bars of the end wall may be thicker (FIGURE 9), similar in thickness (FIGURE 7), or thinner (FIGURE 8) than the gyres of the lateral wall. The widths of the bars may be uniform (FIGURE 8) or variable (FIGURE 15) throughout the length of a perforation plate. A flange or rim of secondary wall frames many simple perforation plates (FIGURE 13) and some multiple perforation plates, especially those with few or widely spaced bars (FIGURES 20, 31). Perforation plates may extend the entire length (FIGURE 26) or only part of the length of the end wall. In the latter category, there is a gradual or abrupt transition from perforations to intervessel pits at the proximal end of the perforation plate (FIGURES 33, 34), at the distal end (FIGURES 8, 9), or at both ends. This character is often highly variable within a sample. End walls also occur in which the perforations do not extend to the lateral margins of the end wall (FIGURE 35). Vessel elements with intervessel pitting on the end wall distal to the perforation plate intergrade with vessel elements in which an extension of the cell continues distally beyond the end wall but is not part of it. Such extensions, called ligules, vary in shape and relative size (FIGURES 36–38). End walls are usually quite straight, but occasionally they are curved or even “saddle-shaped” (FIGURE 39). Perforation plates rarely occur on the lateral walls.

END WALL SLOPE. The histograms of proportional frequencies (FIGURE 41) indicate that slopes of end walls are generally greatest in the petiole, intermediate in the stem, and lowest in the root. The only significant exception to this trend is the phytelphantoid *Ammandra decasperma*, in which clearly discernible vessels were not found in the stem.

Some of the major groups are rather heterogeneous in slopes of end walls (TABLE 1, FIGURE 41). End walls tend to be less oblique in the larger chamaedoreoid species than in the smaller chamaedoreoid species. End walls also tend to be less oblique in the lepidocaryoid lianas than in the other lepidocaryoid palms.

“SPECIALIZATION VALUES.” The diagrams of average specialization values of perforation plates in the major groups of palms indicate that bars in the perforation plates of the wide tracheary elements of the metaxylem are generally most closely spaced in the petiole, intermediate in the stem, and most widely spaced (or fewest) in the root (FIGURE 42). The only significant exception to this tendency is *Ammandra decasperma*, in which clearly discernible vessels were not observed in the stem. The diagrams according to Cheadle’s system (FIGURE 43) show that multiple perforation plates are most frequent in petioles, intermediate in stems, and least frequent in roots.

sel element) or irregular (lower vessel element). 24, reticulate perforation plate: root of *Reinhardtia simplex*, $\times 340$, single large perforation (arrow) surrounded by smaller perforations.



FIGURES 25-31. Wide vessel elements of metaxylem. 25-27, scalariform-reticulate perforation plates: 25, petiole of *Polyandrococos caudescens*, $\times 240$, bars connected by numerous crossbars, both sets of bars very evenly spaced; 26, petiole of *Daemonorops grandis*, $\times 110$, two scalariform configurations appear to be superposed at right angles to form screenlike configuration; 27, petiole of *Arenga undulatifolia*, $\times 180$. 28, scalariform perforation plate: stem of *Clinostigma savaiense*, $\times 88$, bars much branched, especially toward sides of perforation plate; some narrow bars end blindly (arrows). 29, scalariform-reticulate perforation plate: rachis of *Eremospatha* sp., $\times 100$. 30, scalariform perforation plate: stem of *Mauritia vinifera*, $\times 65$, gyres of secondary wall that form bars between the large perforations appear incompletely "fused" to varying degrees. 31, scalariform-reticulate perforation plate: petiole of *Calamus siphonospathus*, $\times 140$, some narrower bars ending blindly (arrows) and peripheral flange of secondary wall.

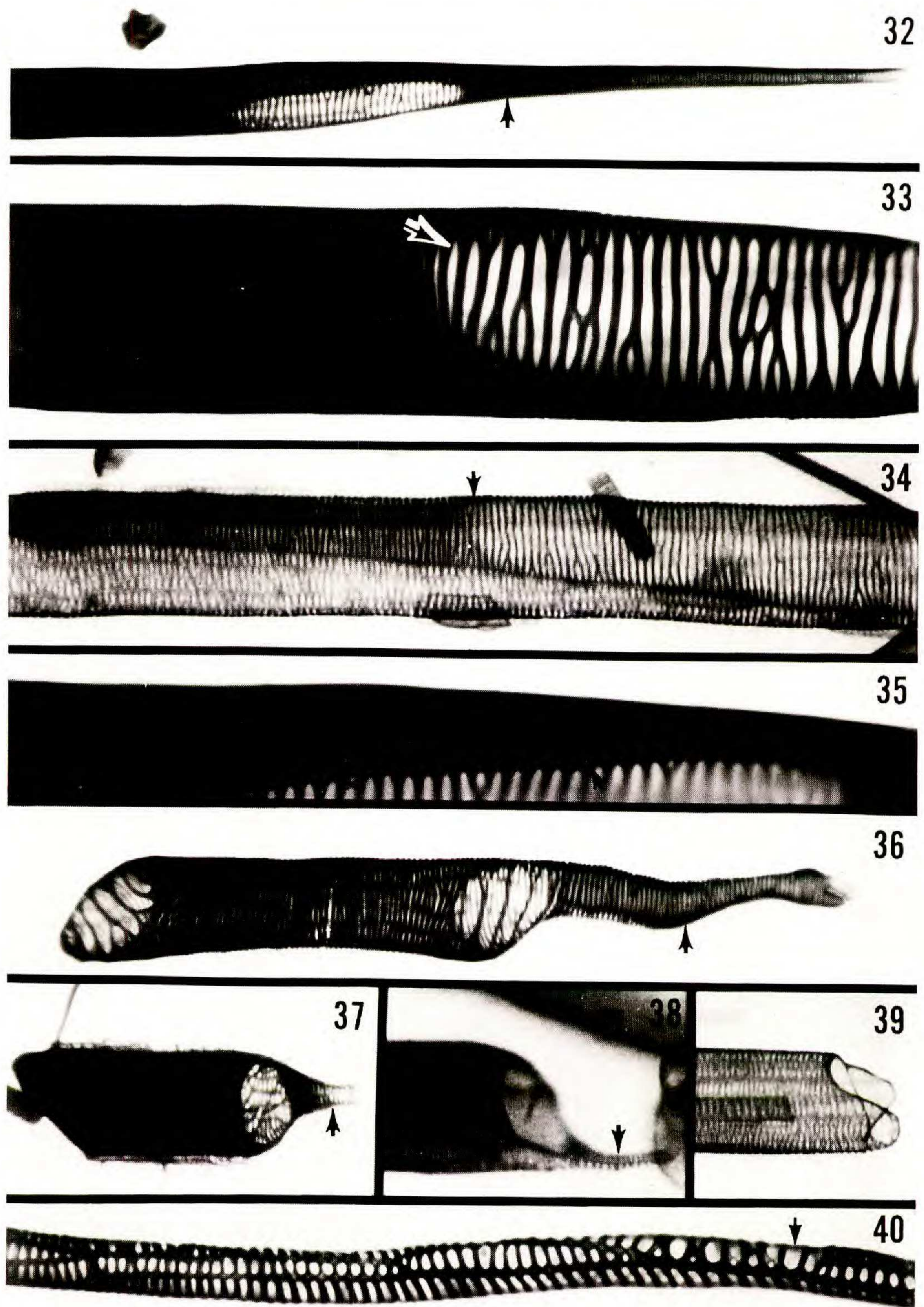
The positions of the major groups in TABLE 2 are generally similar in the two schemes. The major groups are clustered along the continuum of numerical values. At the lower end are the chamaedoreoid (especially the small species) and iriarteoid palms. Above them is a cluster that includes the ceroxylid, arecoid, geonomoid, and phytelephantoid palms. The larger chamaedoreoid species and *Pseudophoenix* are also in or near this cluster. *Nypa* and *Podococcus* belong to one of the two lower clusters of groups in both schemes. The next cluster in the series includes the coryphoid, phoenicoid, caryotoid, and cocosoid palms. The nonscandent lepidocaryoid palms also belong in or near this cluster in both schemes. Finally, at the higher end of the spectrum are the borassoid palms and the lepidocaryoid lianas.

The spacing of bars in perforation plates (FIGURE 42) and the distribution of multiple and simple perforation plates (FIGURE 43) show trends that parallel those shown by the slopes of end walls (FIGURE 40). According to all three criteria, perforation plates are most primitive in the petiole, intermediate (or else similar to either petiole or root) in the stem, and most advanced in the root. This generalization applies to the individual species and to the average values in the major groups. Among the major groups of palms (TABLES 1, 2) the average values of the three criteria indicate that the chamaedoreoid palms (especially the smaller species) are among the most primitive groups. *Nypa* is also fairly primitive, as are the ceroxylid, iriarteoid, arecoid, and geonomoid palms. The coryphoid, borassoid, caryotoid, and cocosoid palms are relatively advanced in their average values, and the lepidocaryoid palms are most advanced of all.

COMPARISON WITH NARROW TRACHEARY ELEMENTS OF THE METAXYLEM. The narrow tracheary elements of the metaxylem are either similar to or more primitive than the wide tracheary elements from the same organ. The narrowest tracheary elements of the metaxylem nearly always appear to be tracheids, on the basis of the configuration of secondary wall. The wider of the narrow tracheary elements of the metaxylem frequently have configurations of secondary wall that indicate either true scalariform perforation plates, or, at least, a series of relatively large pits.

In some specimens with simple perforation plates in the wide vessel elements, some of the narrow tracheary elements of the metaxylem (usually the wider ones) have simple perforation plates. Such cells occur in many of the roots examined and in some stems (e.g., of some coryphoid and lepidocaryoid palms), but not in petioles. The narrow tracheary elements of the metaxylem in such specimens usually contain a closely graded array of forms, from tracheid-like through scalariform configurations to simple perforation plates.

At the other extreme are specimens in which the narrow tracheary elements of the metaxylem all appear to be tracheids on the basis of the configuration of the secondary wall (e.g., petioles of many chamaedoreoid and geonomoid palms). In these specimens, the perforation plates of the wide vessels are primitive.



FIGURES 32-40. Wide tracheary elements of metaxylem. 32, petiole of *Nyssa fruticans*, $\times 95$. End wall (arrow) is slightly curved and continues distally beyond perforation plate to tip of vessel element. 33, petiole of *Cryosophila albida*, $\times 240$. End wall with both perforations (right) and intervessel pits (left). Arrow indicates region where the two types of apertures intergrade. 34, petiole of *Calyptronoma occidentalis*, $\times 360$. End wall with perforations (right) and intervessel pits (left). Arrow indicates region where the two types of apertures intergrade. 35, petiole of *Nyssa fruticans*, $\times 260$. End wall in which perforations do not extend to lateral margin. Arrow indicates row of pitlike aper-

DISCUSSION

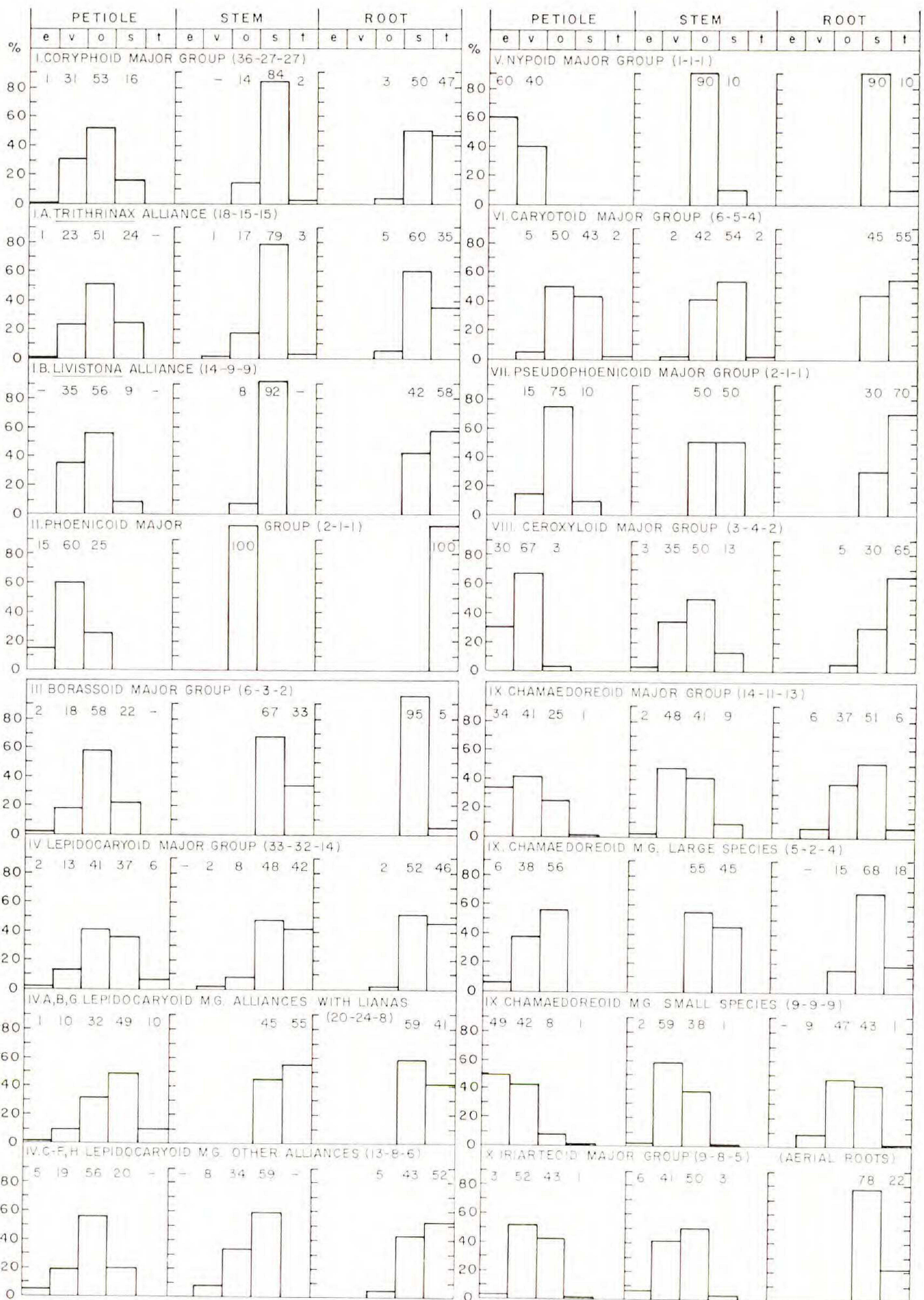
THE TAXONOMIC GROUPS OF PALMS. Many of the major groups of palms differ among themselves in the form of their perforation plates, but the differences are more often average than absolute because of the variability of this character within the groups. Some of the larger major groups comprise alliances with relatively similar averages and/or ranges of variability: the alliances of the coryphoid major group (FIGURES 41–43) and of the cocosoid major group (FIGURES 42, 43), and many of those of the arecoid major group (Klotz, 1977). Some of the major groups contain groups of species of similar habit that are relatively homogeneous in the form of their perforation plates — for example, the small, slender, canelike species of chamaedoreoid palms are almost uniformly primitive in the form of their perforation plates, and the lianoid species of lepidocaryoid palms are all very advanced in this character.

STEMS OF THE PHYTELEPHANTOID PALMS. The reported absence of vessels from the rhizomatous stem of *Ammandra decasperma* may represent some kind of sampling artifact, for great difficulty was encountered in isolating tracheary elements from this specimen. The long, crooked tracheids (?) obtained occur in irregular clusters of 10 to 20 in the vascular bundles. If this species truly lacks vessels in the stem, it exemplifies what Cheadle (1943b) found in certain rhizomatous species in which vessels are lacking in the rhizomes but are present in the other organs of the plant.³

In the short, mostly subterranean stem of *Phytelephas macrocarpa*, Tomlinson (1961) found no vessels but only short, irregular tracheids with pointed ends and angular cross-sectional shape. In the present survey, similar results were obtained in a trunkless specimen of *P. microcarpa* within the intermediate one-third of the diameter of the stem (Klotz, 1975) except that the tracheary elements are long, and some of them exhibit regions of possible scalariform perforations on the lateral walls (FIGURE 40). However, a different collection of the same species yielded unequivocal vessels along with many tracheids from the center of the short stem. The vessel elements resemble those from the erect, emergent stems of *Phytelephas* sp. (*Moore & Dransfield 10224* — not included in the tabulations for this study) and another phytelephantoid species, *Palandra aequatorialis*.

tures lateral to perforations on end wall. 36, stem of *Sindroa longisquama*, × 88. Arrow indicates long, broad ligule. 37, stem of *Elaeis oleifera*, × 88. Arrow indicates short, broad ligule. 38, stem of *Itaya amicornum*, × 160. Arrow indicates slender ligule. 39, root of *Aiphanes* sp., × 100. "Saddle-shaped" end wall. 40, tracheary element from stem of *Phytelephas microcarpa*, × 240. Arrow indicates possible perforation plate.

³ However, a maceration from the same stem in the slide collection of P. B. Tomlinson includes tracheary elements with regions of possible scalariform perforations on the lateral walls (as in FIGURE 40).



PHYLOGENETIC IMPLICATIONS. The most primitive xylem in palms is not found in the coryphoid major group, which contains the greatest number of other primitive characters, but in more advanced groups such as the nypoid, chamaedoreoid, iriarteoid, podococcoid, and arecoid palms. In the evolutionary line comprising the pseudophoenicoid, ceroxyloid, and chamaedoreoid major groups (Moore, 1973), the small chamaedoreoid palms have the most primitive xylem, yet include the genera most advanced

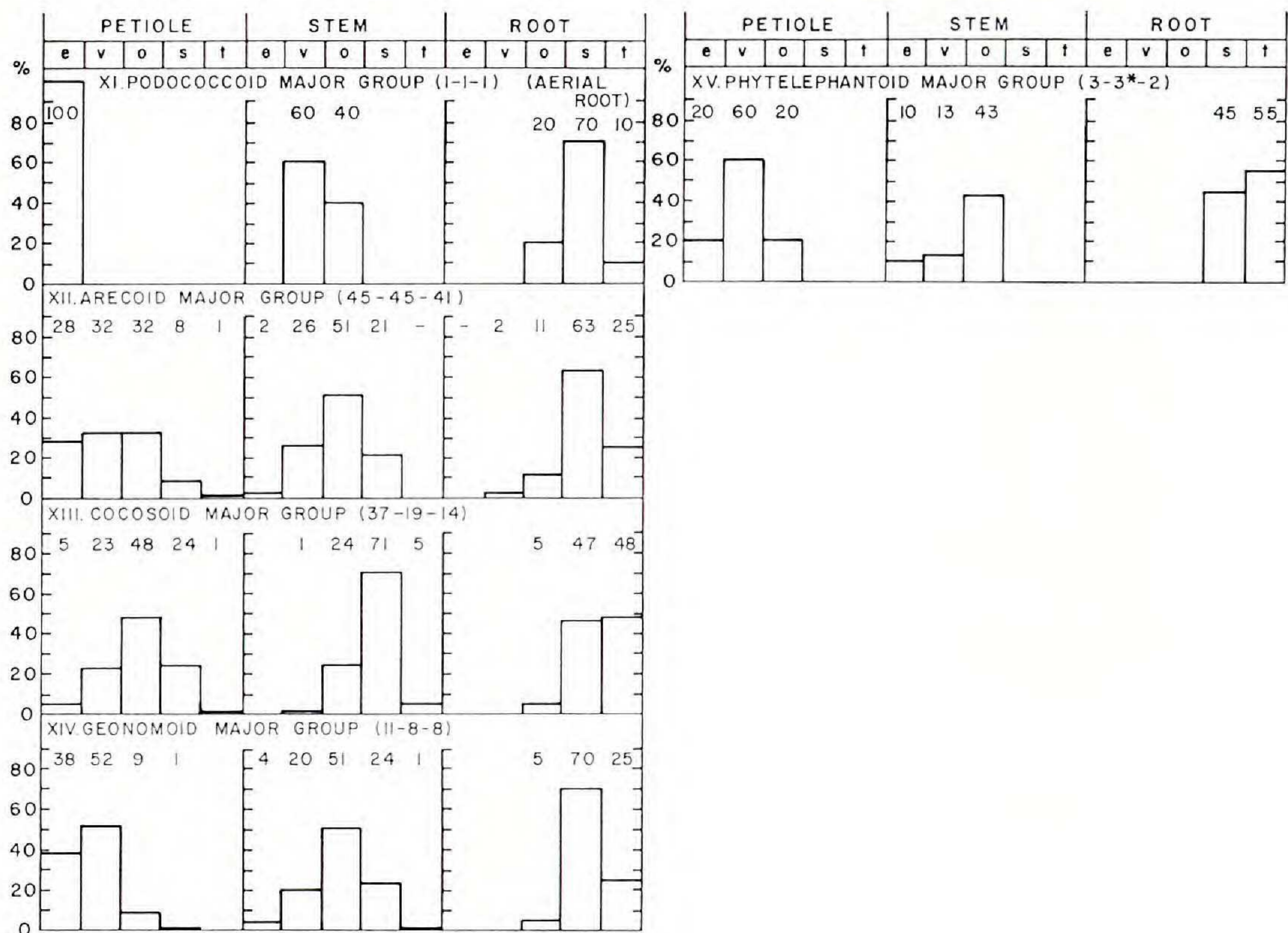


FIGURE 41. End wall slopes of wide tracheary elements of metaxylem: histograms of proportional frequencies of the five categories of slope. Proportional frequencies (as percentages) printed under their respective categories. Values of less than one percent recorded as a dash (-). Numbers of specimens examined in each group for petiole, stem, and root in parentheses. * Including *Ammandra* (= 0).

in other characters. *Pseudophoenix*, the most primitive genus in this evolutionary line, has xylem that is much more advanced than that in the small chamaedoreoid palms.

On the other hand, within the coryphoid major group, the most primitive xylem occurs in the *Trithrinax* alliance, which does contain the greatest number of other primitive features. *Nypa fruticans*, the sole species of nypoid palm, possesses a mixture of primitive and advanced features, including primitive xylem. The iriarteoid, podococcoid, and arecoid palms generally have more primitive xylem and are more primitive in other ways than are the cocosoid palms.

There is little resemblance between Moore's (1973) systematic sequence of the evolutionary lines and major groups and the sequence in the present study based on the average level of evolution of the xylem. This result is not surprising, for different selective pressures would be exerted on xylem than are exerted, for example, on the reproductive parts of the plant such as the inflorescences, flowers, and fruits. Evolution in the xylem appears to have progressed independently in the various taxonomic groups of palms.

ECOLOGICAL IMPLICATIONS REGARDING HABITAT. Carlquist (1975) hypothesized that perforation plates with few or no bars generally represent a more favorable adaptation to environmental conditions of greater average moisture demand than do perforation plates with more numerous bars that are more closely spaced. To some extent, the palms tend to display this correlation between form of perforation plates and degree of moisture demand in the environment, at least as a general trend among the major groups. For example, the coryphoid, phoenicoid, borassoid, pseudophoenicoid, and cocosoid palms include many species adapted to habitats that are very exposed (e.g., savannas) or that have low or strongly seasonal precipitation (Moore, 1973). These groups tend to have fewer, more widely spaced bars in the perforation plates than do some of the groups that are mainly adapted to more mesic habitats such as rain forest, cloud forest, or forest understory — e.g., ceroxylid, chamaedoreoid, iriarteoid, podococcoid, arecoid, geonomoid, and phytelephantoid palms. *Nypa fruticans*, which inhabits estuaries in the humid tropics of the Old World, also fits with the latter groups regarding form of perforation plates (Carlquist, 1975). Most lepidocaryoid and caryotoid palms are adapted to tropical regions of high rainfall (Moore, 1973), but the moderately to very advanced perforation plates that characterize these species may be related to the fact that many of them inhabit forests at low elevations and must therefore tolerate the greater moisture demand that would accompany a warmer climate. However, the discrepancies that various species and higher groups of palms present with regard to these trends indicate that the relationship between form of perforation plates and adaptation to the moisture regime of the environment is not simple. For example, the lianas of the lepidocaryoid and cocosoid major groups are adapted to similar kinds of habitats yet differ markedly in the form of their perforation plates, especially in the stem. Among the arborescent species of wet lowland tropical forests, certain coryphoid palms (e.g., *Cryosophila albida*, *Itaya amicum*, *Licuala muelleri*) have more advanced perforation plates (especially in stem and root) than do iriarteoid palms of comparable or greater size.

HABIT CATEGORIES. Few consistent relationships occur between the habits of palms and the forms of their perforation plates.⁴ Among the species of lianas, the sequence of kinds of perforation plates in the organs of the plant corresponds to the modal or average condition of this character within the major group to which the species belongs. For example, only multiple perforation plates occur in the wide vessel elements of the scandent species *Chamaedorea elatior*, as in the nonscandent small chamaedoreoid palms. Species of the cocosoid genus *Desmoncus* are lianas with only multiple perforation plates in the wide vessel elements of the shoot and simple perforation plates in the wide vessel elements of the root. The sequence of kinds of perforation plates in *Desmoncus* falls within the lower part of the range of this character exhibited by the cocosoid major group. The

⁴ In contrast, there are relationships between the habits of palms and the dimensions of their vessel elements, especially the diameters of the wide vessels in the stem (Klotz, 1977, 1978).

lepidocaryoid lianas are very advanced in the form of their perforation plates (FIGURES 41–43). They fall within the upper part of the range of this character in the lepidocaryoid major group.

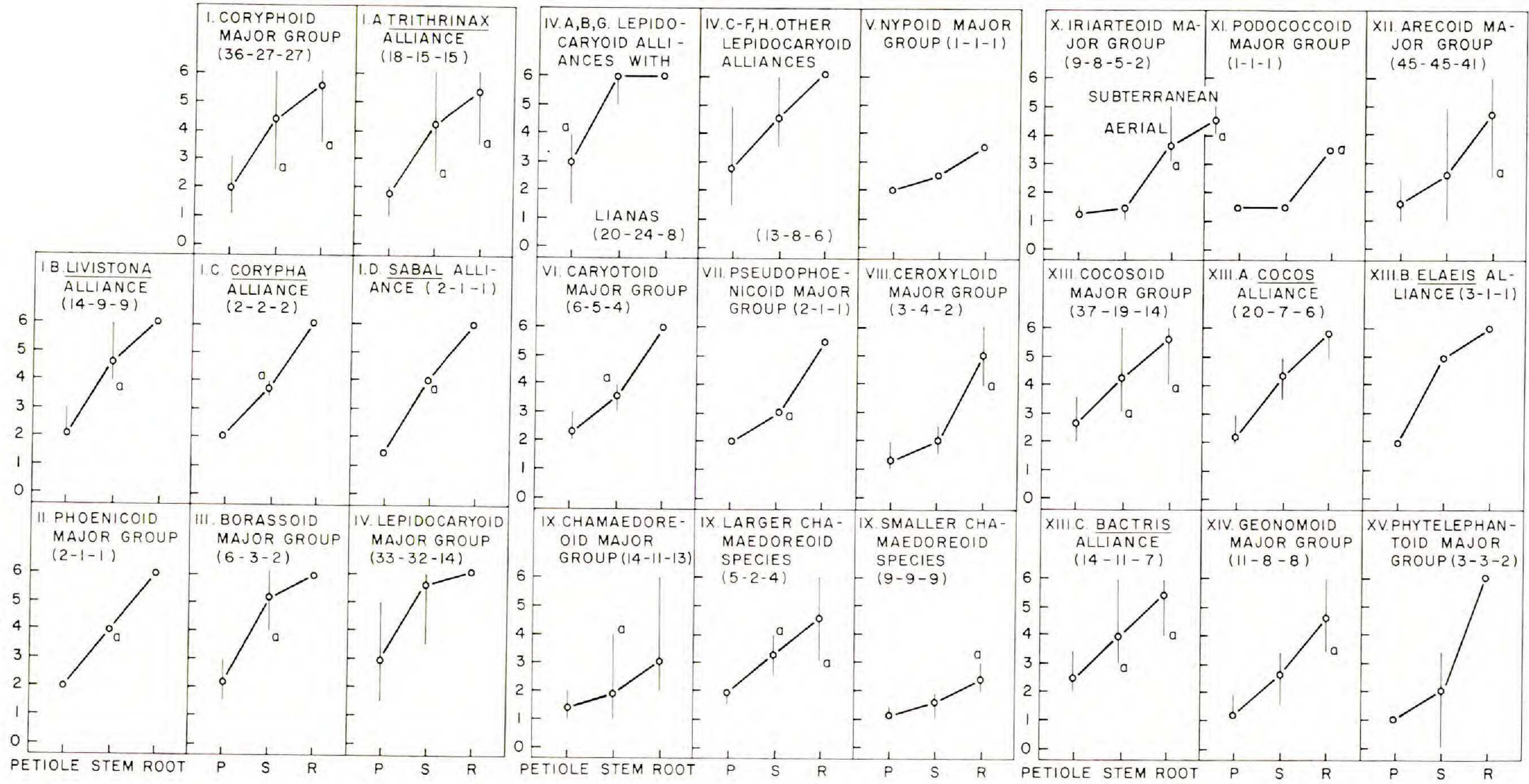
The same tendency exhibited by the lianas is also shown by the rhizomatous palms, which occur in several of the major groups. Perforation plates of the wide vessel elements of the metaxylem are all multiple in the rhizomatous stems of *Sclerosperma manni* (arecoid), *Calyptrogyne brachystachys* (geonomoid), and *Phytelephas microcarpa* (phytelephanoid). They are mixed multiple and simple in the coryphoid palms *Rhaphidophyllum hystrix*, *Licuala* sp., and *Serenoa repens*; and in the cocosoid palms *Allagoptera arenaria* and *Elaeis oleifera*. Finally, they are mostly simple in the lepidocaryoid *Eleiodoxa conferta*.

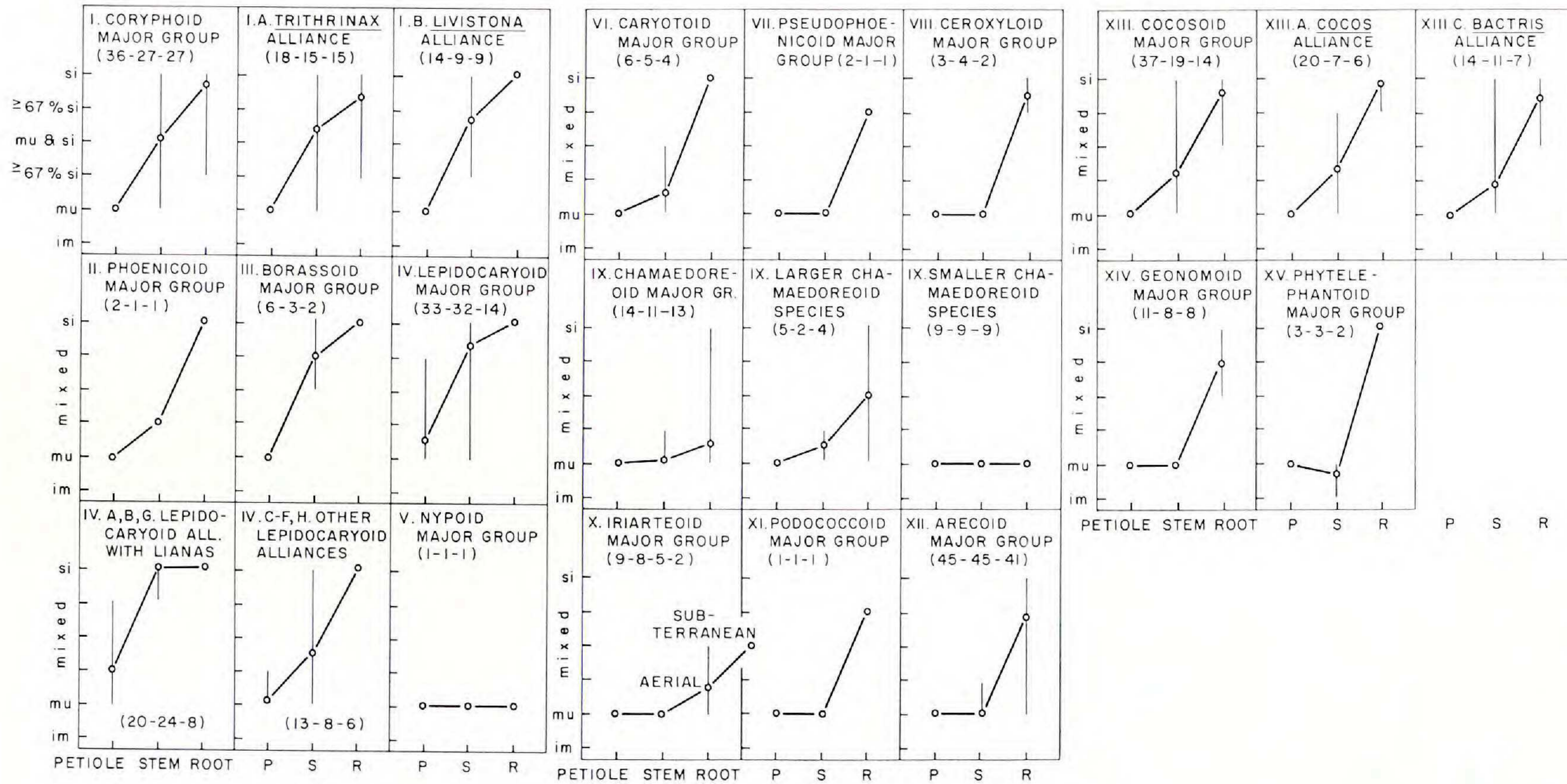
The remaining category includes all palms with erect, nonscandent stems. It is thus a very diverse group of arborescent, shrubby, and dwarf species. In this group, the small, slender species of the forest understory usually have the most primitive perforation plates within their respective major groups. This tendency is exhibited among the coryphoid palms (*Rhapis excelsa*), the lepidocaryoid palms (*Lepidocaryum* spp.), the chamaedoreoid palms (*Synechanthus* spp., *Chamaedorea* spp., *Wendlandiella polyclada*), the arecoid palms (*Reinhardtia simplex*, *Pinanga* sp., *Iguanura* sp., and others), the cocosoid palms (*Aiphanes* sp., *Bactris simplicifrons*), and the geonomoid palms (*Pholidostachys pulchra*, *Geonoma* spp.). Conversely, the most advanced perforation plates in some of the major groups occur among the larger species of those major groups — for example, *Pigafetta filaris* (lepidocaryoid); *Hyophorbe indica* (chamaedoreoid); *Manicaria saccifera*, *Roystonea* spp. (arecoid); and *Welfia georgii* (geonomoid).

DATA OF OTHER AUTHORS. Cheadle (1942) found only scalariform perforation plates in the metaxylem of leaves (22 species of palms) and inflorescence axes (6 species). In aerial stems, he found 15 species with scalariform perforation plates only and 8 species with a mixture of scalariform and simple perforation plates. In roots, all 21 species that he examined had a mixture of scalariform and simple perforation plates in the metaxylem, although the scalariform perforation plates were generally restricted to the early-matured metaxylem. The present study reports petioles that contain simple perforation plates and roots that lack simple perforation plates. Thus Cheadle's (1942) findings are similar to those of the present study except that he found fewer kinds of perforation plates within leaves and roots of palms.

Mahabalé (1959) observed the range of numbers of perforation plate bars in stems of 14 species of palms, including 8 species of *Phoenix*. Most of his data fit within the limits of the variation observed for the major groups in the present study.

Tomlinson's (1965) brief summary of his unpublished findings on perforation plates in palm stems presents a sequence for the taxonomic groups according to their average level of evolution in this character. His





FIGURES 42, 43. Specialization values of wide tracheary elements of metaxylem. 42 (above), according to author's method; 43 (below), according to Cheadle's method. Numbers of specimens examined of petiole, stem, and root, respectively, in parentheses under the name of each group.

sequence of groups is similar to the ones that are set forth in the present study (TABLES 1, 2) except that he lists the phytelephantoid palms as lacking vessels in the stem. He found the chamaedoreoid and iriarteoid palms to be "least specialized"; the "Arecoïd" (including geonomoid), nypoid, and phoenicoid palms to be "unspecialized"; the caryotoid, cocosoid (including "Cocoid" and "Bactroid"), coryphoid (as "Sabaloid"), and nonscandent lepidocaryoid palms to be "moderately specialized"; and the borassoid and scandent lepidocaryoid palms to be "most specialized." Tomlinson's data on the forms of perforation plates in various species of palms (Tomlinson, 1961; 1966; 1969; unpublished data) generally agree with the trends expressed for the major groups in the present study.

TYPES OF VASCULAR BUNDLES. In their survey of monocotyledons, Cheadle and Uhl (1948) found that as the wide vessel elements of the metaxylem became more advanced, "they became larger in relation to the remaining elements in the metaxylem." In petioles of palms, the most primitive wide vessel elements (i.e., those with the narrowest perforations) occur in bundles of types IIIA and IV rather than type I, which is considered to be the most primitive bundle type. The species with type I bundles predominating in the petiole have wide vessel elements of metaxylem in which the bars of the perforation plates tend to be slightly more widely spaced (Klotz, 1977). However, this exception to the relationship stated by Cheadle and Uhl (1948) is relatively minor. The present observations in palms generally support the conclusions of these authors.

SUMMARY

Perforation plates of the wide vessels of metaxylem from the petiole (209 species), the central part of the stem (169 species), and the root (136 species) were examined in representative species from all of the major groups of palms. In nearly all of the species examined, the bars of the perforation plates are most closely spaced in the petiole, most widely spaced in the root, and intermediate (or else similar to either petiole or root) in the stem. End walls of the wide vessel elements are most oblique in the petiole, least oblique in the root, and intermediate in the stem. Differences in the form of the perforation plates among the taxonomic groups are mostly average or partial rather than absolute. *Nyssa* has multiple perforation plates in all three organs. Iriarteoid and most chamaedoreoid palms have multiple perforation plates in all organs, but some species also have simple perforation plates in the roots. Ceroxyloid, geonomoid, most arecoïd, and most phytelephantoid palms have either simple or mixed multiple and simple perforation plates in the roots and only multiple perforation plates in the shoots. Caryotoid, most cocosoid, and most coryphoid palms have simple perforation plates in the roots, multiple or mixed multiple and simple perforation plates in the stems, and multiple perforation plates in the petioles. Lepidocaryoid palms have multiple, mixed multiple and simple, or simple perforation plates in the stems, and multiple or mixed multiple and simple perforation plates in the

petioles. The form of the perforation plates is not strictly correlated with habit. For example, the lepidocaryoid lianas all have simple perforation plates in the stems, but only multiple perforation plates occur in the stems of the cocosoid and chamaedoreoid lianas. The form of the perforation plates shows only partial or inconsistent correlation with environmental moisture regime and with evolutionary advancement in other characters.

ACKNOWLEDGMENTS

This study is part of a dissertation submitted in partial fulfillment of the requirements for a Ph.D. degree at Cornell University. The author is grateful to Drs. M. V. Parthasarathy and H. E. Moore, Jr. for their guidance and assistance during the course of the project, and to Drs. N. W. Uhl, J. M. Kingsbury, P. B. Tomlinson, J. B. Fisher, and V. I. Cheadle for valuable discussion. The study was supported in part by funds from Hatch Project #407. Dr. H. P. Banks permitted the use of his Zeiss Photomicroscope for some of the photomicrography.

LITERATURE CITED

- CARLQUIST, S. 1975. Ecological strategies of xylem evolution. xi + 259 pp. Univ. California Press, Berkeley.
- CHEADLE, V. I. 1942. The occurrence and types of vessels in the various organs of the plant in the Monocotyledoneae. *Am. Jour. Bot.* **29**: 441-450.
- . 1943a. The origin and certain trends of specialization of the vessel in the Monocotyledoneae. *Ibid.* **30**: 11-17.
- . 1943b. Vessel specialization in the late metaxylem of the various organs in the Monocotyledoneae. *Ibid.*: 484-490.
- & H. KOSAKAI. 1975. Vessels in Juncales: II. Centrolepidaceae and Restionaceae. *Am. Jour. Bot.* **62**: 1017-1026.
- & N. W. UHL. 1948. Types of vascular bundles in the Monocotyledoneae and their relation to the late metaxylem conducting elements. *Am. Jour. Bot.* **35**: 486-496.
- ESAU, K. 1965. Plant anatomy. ed. 2. xx + 767 pp. John Wiley & Sons, New York.
- FISHER, J. B. 1975. Environmental impact of lethal yellowing disease of coconut palms. *Environ. Conserv.* **2**: 299-304.
- JOHANSEN, D. A. 1940. Plant microtechnique. xi + 523 pp. McGraw-Hill, New York.
- KLOTZ, L. H. 1975. Specialization of late metaxylem tracheary elements in palms. P. 45 in Abstracts of papers to be presented at the meetings of the Botanical Society of America and certain affiliated groups at Oregon State University, Corvallis. [Abstract.]
- . 1977. A systematic survey of the morphology of tracheary elements in palms. viii + 221 pp. Unpubl. Ph.D. Thesis, Cornell University, Ithaca, N.Y.
- . 1978. Observations on diameters of vessels in stems of palms. *Principes* (in press).
- MAHABALÉ, T. S. 1959. Resolution of the artificial palm genus, *Palmoxylon*: a new approach. *Palaeobotanist* **7**: 76-84.

- MOORE, H. E., JR. 1973. The major groups of palms and their distribution. *Gent. Herb.* 11: 27-141.
- & N. W. UHL. 1973. Palms and the origin and evolution of monocotyledons. *Quart. Rev. Biol.* 48: 414-436.
- PARTHASARATHY, M. V., & L. H. KLOTZ. 1976. Palm "wood." I. Anatomical aspects. *Wood Sci. Tech.* 10: 215-229.
- TOMLINSON, P. B. 1961. Anatomy of the monocotyledons, II. *Palmae*. (C. R. METCALFE, ed.) xv + 453 pp. Clarendon Press, Oxford.
- . 1965. Trends in cell dimensions in palms. *Am. Philos. Soc. Yearb.* 1965: 354, 355.
- . 1966. Notes on the vegetative anatomy of *Aristeyera spicata* (*Palmae*). *Jour. Arnold Arb.* 47: 23-29.
- . 1969. The anatomy of the vegetative organs of *Juania australis* (*Palmae*). *Gent. Herb.* 10: 412-424.
- & M. H. ZIMMERMANN. 1967. The "wood" of monocotyledons. *Int. Assoc. Wood Anat. Bull.* 1967(2): 4-24.
- ZIMMERMANN, M. H. 1978. Structural requirements for optimal water conduction in tree stems. *In*: P. B. TOMLINSON & M. H. ZIMMERMANN, eds., *Tropical trees as living systems*. Cambridge Univ. Press, New York (in press).

SECTION OF GENETICS
DEVELOPMENT AND PHYSIOLOGY
CORNELL UNIVERSITY
ITHACA, NEW YORK 14853

PRESENT ADDRESS:
HARVARD FOREST
PETERSHAM,
MASSACHUSETTS 01366